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THE ORIGIN OF LUNGS, A CHAPTER IN EVOLUTION.

BY CHARLES MORRIS.

The air bladder of fishes is an organ whose true purpose has long been classed among the mysteries of animal organization. All we know about it is the duty to which it is now occasionally devoted; but there is abundant reason to believe that this was not its original function. This duty is indicated by its frequent title of "swim-bladder," the organ being seemingly used to some extent to aid the fish in swimming. Cuvier tells us that "the most obvious use of the swim-bladder is to keep the animal in equilibrium with the water, or to increase or reduce its relative weight, and thereby cause it to ascend or sink, in proportion as that organ is dilated or compressed." In addition it may be of use, as Günther observes, "in raising the fore-part of the body or depressing it, as occasion may require."

Doubtless all this is correct, but that the bladder was evolved for such a purpose, or is of any essential utility as a swimming organ, there is the strongest reason to question; and in all probability its original purpose was something quite different. As it at present exists it is often too small to be of use in changing the gravity of the fish, and in many cases it is entirely absent. In others, its compressing muscles, as Van der Hœven states, seem incapable of being used to expand it. Yet in all these cases the fish seems at no disadvantage in swimming as compared with those that possess large and

efficient bladders. As an instance may be cited the mackerel, which has no bladder, yet which certainly finds no difficulty in rising or sinking. The same may be said of the great shark tribe, which is bladderless. All this goes to indicate that the air bladder could not have been developed originally for such a purpose, since its use as a swim-bladder seems of such little value to the fish that it has been frequently suffered to degenerate and disappear, and even if such a service were essential to the fish tribe it is impossible to conceive that this organ could have been of utility in swimming in the earlier stages of its development.

Before considering, however, the question of the original purpose of the air-bladder, some description of its present conditions is necessary. This organ is an internal sac, possessed by many, but not by all, fishes, and is situated ordinarily in the dorsal region of the body, between the vertebræ and the intestines, and in front of the kidneys. It lies outside the peritoneal sac, a fold of which invests its ventral surface. Its relation to the surrounding organs varies. In many cases it is intimately adherent to the vertebral column and the abdominal tissues, and is often enclosed in osseous capsules formed by the vertebræ. In such cases it may readily be compressed or expanded, and the weight of the fish in relation to the water be thus changed. But in other instances it is almost loose in the abdominal cavity, and seemingly incapable of acting as a gravity organ.

It varies greatly both in size and form. In some fishes it is so large as to extend into the tail, while in other instances it sends processes into the head; these having some connection with the organ of hearing. In many fishes, on the contrary, it is small, sometimes so minute as to be of no conceivable utility. In numerous instances it is entirely absent. And here we find the highly significant fact that variations of this kind occur in closely related species. Thus, as has been already said, the mackerel has no air-bladder. Yet one exists in *Scomber pneumatophorus*, a species which in every other respect closely resembles the mackerel. Similarly in the genus *Polynemus* one species (*paradiseus*) is destitute of an air-

bladder, while every other species possesses one. A like singular variation occurs in the case of related genera. In the genus *Sebastes* the air-bladder is very large, yet in a closely related genus it is scarcely the size of a pea.

Its variations in form are equally marked. Ordinarily it is a simple sac, with smooth interior. Yet in some instances it has a cellular interior, and in others it is divided by transverse partitions into from two to four sections. In other cases it is divided by a longitudinal partition into two lateral halves. In some families there is a remarkable development of lateral appendages, of varying character. In others the internal sacculation becomes so great that the bladder resembles the batrachian lung, and evidently does duty in the breathing of air.

The bladder itself is composed of two layers of membrane, the outer one being usually provided with muscular fibres, while the inner one is abundantly supplied with blood vessels. These take the form of capillary plexuses, or what are known as *retia mirabilia,* whose purpose may be to secrete the gas with which the bladder is filled. This gas differs in character in different fishes. In fresh-water fishes it is nearly pure nitrogen, the percentage of oxygen being small. In marine fishes, on the contrary, oxygen is in excess. This is particularly the case in the deep-swimmers, in some of which the bladder has been found to contain as much as eighty-seven per cent. of oxygen.

These gaseous contents, if, as seems probable, obtained through secretion by the blood vessels, are not always so obtained, for in many fishes an arrangement exists by which air may directly enter the bladder from without. This is what is known as the pneumatic duct, a tubular connection between the œsophagus and the air-bladder, not unlike that which supplies the lungs of air-breathers. This duct presents the same remarkable variability which we have observed in other characteristics of the air-bladder. Its point of connection with the alimentary tract varies, being usually in the œsophagus, but in some fishes as far back as the stomach. In the Ganoid order of fishes the duct is a short one, and always

open. In the Physostome order it is longer, and in many instances is closed, it being occasionally reduced to a fine filament. In the other orders of Teleostean fishes, which embrace the great majority of species, the pneumatic duct does not exist. Whatever function this duct may have once performed, therefore, it seems as a rule to have lost its utility. That its function was an essential one in the early stage of fish life is rendered evident by the fact that all fishes which have a bladder at all possess a pneumatic duct in the larval stage of growth, this duct, in most cases, vanishing as they grow older.

If now we seek to discover the original purpose of this organ, there is abundant reason to believe that it had nothing to do with swimming. Certainly the great family of the sharks, which have no bladder, are at no disadvantage in changing their depth or position in the water. Yet if the bladder is necessary to any fish as an aid in swimming, why not to all? And if this were its primary purpose, how shall we explain its remarkable variability? No animal organ with a function of essential importance presents such extraordinary modifications in related species and genera. In the heart, brain, and other organs there is one shape, position, and condition of greatest efficiency, and throughout the lower forms we find a steady advance towards this condition. Great variation, on the other hand, usually indicates that the organ is of little functional importance, or that it has lost its original function. Such we conceive to be the case with the air-bladder. The fact of its absence from some and its presence in other fishes of closely related species, goes far to prove that it is a degenerating organ; and the same is shown by the fact that it is useless in some species for the purpose to which it is applied in others. That it had, at some time in the past, a function of essential importance there can be no question. That it exists at all is proof of this. But its modern variations strongly indicate that it has lost this function, and is on the road towards extinction. Larval conditions show that it had originally a pneumatic duct as one of its essential parts, but this has in most cases disappeared. The bladder itself has in many cases partly or wholly disappeared. Where preserved, it seems to be through

its utility for some secondary purpose, such as an aid in swimming or in hearing. That its evolution began very long ago there can be no question; and the indications are that it began long ago to degenerate, through the loss of its primitive function.

What was this primitive function? In attempting to answer this question we must first consider the air-bladder in relation to the fish tribe as a whole. In one principal order of fishes, the Elasmobranchs, the air-bladder does not exist. No shark or ray possesses this organ. In some few sharks, indeed, there is a diverticulum of the pharynx which may be a rudimentary approach to the air-bladder; but this is very questionable. The conditions of its occurrence in the main body of modern fishes, the Teleostean, we have already considered. But in the most ancient existing order of fishes, the Ganoids, of which but a few representatives remain, it exists in an interesting condition. In every modern Ganoid the air-bladder has an effective pneumatic duct, which usually opens into the dorsal side of the œsophagus, but in the sub-order Polypterus opens, like the wind-pipe of lung-breathers, into the ventral side. Finally, in the small sub-order of Dipnoi, also a survivor from the remote past, the duct not only opens ventrally into the œsophagus, but the air-bladder does duty as a lung. Externally it differs in no particular from an air-bladder; but internally it presents a cellular structure which nearly approaches that of the lung of the bactrachians. There are three existing representatives of the Dipnoi. One of these, the Australian lung-fish (*Ceratodus*), has a single bladder, which, however, is provided with breathing pouches having a symmetrical lateral arrangement. It has no pulmonary artery, but receives branches from the *Arteria cœliaca.* In the other two forms, *Lepidosiren* and *Protopterus,*—the kindred "mud fishes" of the Amazon basin and tropical Africa,—the bladder or lung is divided into two lateral chambers as in land animals, and is provided with a separate pulmonary artery.

The opinion seems to be tacitly entertained by physiologists that this employment of the air-bladder by the Dipnoi as a

lung is a secondary adaptation, a side issue from its original purpose. To this I venture to oppose the theory (which I have already offered in the "Proceedings" of the Academy of Natural Sciences of Philadelphia) that it is the original purpose, and that its degeneration is due to the disappearance of the necessity of such a function. As regards the gravitative employment of the bladder, the Teleostean fishes, to which this function is confined, are of comparatively modern origin; while the Dipnoi are surviving representatives of a very ancient order of fishes, which flourished in the Devonian age of geology, and in all probability breathed air then as now; and the Ganoids, which approach them in this particular, are similarly ancient in origin, and were the ancestors of the Teleosteans. The natural presumption, therefore, is that the duty which it subserved in the most ancient fishes was its primitive function.

The facts of embryology lend strong support to this hypothesis. For the air-bladder is found to arise in a manner very similar to the development of the lung. They each begin as an outgrowth from the fore-part of the alimentary tract, the only difference being that the air-bladder usually rises dorsally and the lung ventrally. The fact already cited, that the pneumatic duct is always present in the larval form, in fishes that possess a bladder, is equally significant. All the facts go to show that the introduction of external air into the body was a former function of the air-bladder, and that the atrophy of the duct in many cases, and the disappearance of the bladder in others, are results of the loss of this function.

Such an elaborate arrangement for the introduction of air into the body could have, if we may judge from analogy, but one purpose, that of breathing, to which purpose the muscular and other apparatus for compressing and dilating the bladder, now seemingly adapted to gravitative uses, may have been originally applied. The same may be said of the great development of blood capillaries in the inner tunic of the bladder. These may now be used only for the secretion of gas into its interior, but were perhaps originally employed in the respiratory secretion of oxygen. In fact, all the circum-

stances mentioned—the similarity in larval development between bladder and lung, the larval existence of the pneumatic duct, the arrangements for compressing and dilating the bladder, and the capillary vessels on its inner tunic—point to the breathing of air as its original purpose.

It is probable that the Ganoid, as well as the Dipnoid, bladder, is to some extent still used in breathing. The Dipnoi have both lungs and gills, and probably breathe with the latter in ordinary cases, but use their lungs when the inland waters in which they live become thick and muddy, or are charged with gases from decomposing organic matter. The Ganoid fishes to some extent breathe the air. In *Polypterus* the air-bladder resembles the Dipnoid lung in having lateral divisions, and a ventral connection with the œsophagus, while in *Lepidosteus* (the American Gar Pike) it is cellular and lung-like. This fish keeps near the surface, and may be seen to emit air-bubbles, probably taking in a fresh supply of air. The American Bow-Fin or Mud Fish (*Amia*) has a bladder of the same lung-like character, and has been seen by Wilder to come to the surface, open its jaws widely, and apparently swallow a large quantity of air. He considers that both *Lepidosteus* and *Amia* inhale and exhale air at somewhat regular intervals, resembling in this the salamanders and tadpoles, "which, as the gills shrink and the lungs increase, come more frequently to the surface for air."

As the facts stand there is no evident line of demarcation between the gas-containing bladders of many of the Teleosteans, the air-containing bladders of others and of the Ganoids, and the lung of the Dipnoi, and the indications are in favor of their having originally had the same function, and of this being the breathing of air.

If now we ask, what were the conditions of life under which this organ was developed, and what the later conditions which rendered it of no utility as a lung, some definite answer may be given. The question takes us back to the Devonian and Silurian geological periods, during which the original development of the bladder probably took place. In this era the seas were thronged with fishes of two distinct orders, the Elasmo-

branchs and the Dipnoi, with the Ganoids as a branch of the true fishes. The former were without, the latter with, an air-bladder; a difference in organization which was most likely due to some marked difference in their life habits. The Elasmobranchs were the monarchs of the seas, against whose incursions the Ganoids put on a thick protective armor, and probably sought the shallow shore waters, while their foes held chief possession of the deeper waters without.

We seem, then, to perceive the Ganoid fishes driven by their foes into bays and estuaries and the waters of shallow coasts, ascending streams, and dwelling in inland waters. Here two influences probably acted on them. The waters they dwelt in were often thick with sediment, and were doubtless in many instances poorly aerated, rendering gill-breathing difficult. And the land presented conditions likely to serve as a strong inducement to fishes to venture on shore. Its plant life was abundant, while its only animal inhabitants seem to have been insects, worms, and snails. There can be little doubt that the active fish forms of that period, having no enemies to fear on the land, and much to gain, made active efforts to obtain a share of this vegetable and animal food. Even to-day, when they have numerous foes to fear, many fishes seek food on the shore, and some even climb trees for this purpose. Under the conditions of the period mentioned there was a powerful inducement for them to assume this habit.

Such conditions must have strongly tended to induce fishes to breathe the air, and have acted to develop an organ for this purpose. In addition to the influences of foul or muddy water and of visits to land, may be named that of the drying-out of pools, by which fishes are sometimes left in the moist mud till the recurrence of rains, or are even buried in the dried mud during the rainless season. This is the case with the modern Dipnoi, which use their lungs under such circumstances. In certain other fresh-water fishes, of the family Ophiocephalidæ, air is breathed while the mud continues soft enough for the fish to come to the surface, but during the dry period the animal remains in a torpid state. These fishes have no lungs, but breathe the air into a simple cavity in the pharynx, whose

opening is partly closed by a fold of the mucous membrane. Another family, the Labyrinthici, of similar habits, possesses a more developed breathing organ. This is a cavity formed by the walls of the pharynx, in which are thin laminæ or plates, which undoubtedly perform an oxygenating function. The most interesting member of this family is *Anabas scandens*, the Climbing Perch. In this fish, which not only leaves the water, but climbs trees, the air-breathing organ is greatly developed. The Labyrinthici moreover have usually large air-bladders. As regards the occasional breathing of air by fishes, even in species which do not leave the water, it is quite common, particularly among fresh-water species. Cuvier remarks that air is perhaps necessary to every kind of fish; and that, particularly when the atmosphere is warm, most of our lacustrine species sport on the surface for no other purpose.

It is not difficult to draw a hypothetical plan of the development of the air-bladder as a breathing organ. In the two families of fishes just mentioned, whose air-bladders indicate that they once possessed the air-breathing function and have lost it, we perceive the process of formation of an air-breathing organ beginning over again, under stress of similar circumstances. The larval development of the air-bladder points significantly in the same direction. In fact, we have strong reason to believe that air-breathing in fishes was originally performed, as it probably often is now, by the unchanged walls of the œsophagus. Then these walls expanded inwardly, forming a simple cavity, partly closed by a fold of membrane, like that of the Ophiocephalidæ. A step further reduced this membraneous fold to a narrow opening, leading to an inner pouch. As the air-breathing function developed, the opening became a tube, and the pouch a simple lung, with compressing muscles and capillary vessels. By a continuation of the process the smooth-walled pouch became sacculated, its surface being increased by folding into breathing cells. Finally a longitudinal constriction divided it into two lateral pouches, such as we find in the lung of the Dipnoi. This brings us to the verge of the lung of the Batrachia, which is but a step in

advance, and from that the line of progress is unbroken to the more intricate lung of the higher land animals.

The dorsal position of the bladder and its duct would be a difficulty in this inquiry, but for the fact that the duct is occasionally ventral. This dorsal position may have arisen from the upward pressure of air in the swimming fish, which would tend to lift the original pouch. But in the case of fishes which made frequent visits to the shore, new influences must have come into play. The effect of gravity tended to draw the organ and its duct downward, as we find in one family of the Ganoids and in all the Dipnoi; and its increased use in breathing required a more extended surface. Through this requirement came the pouched and cellular lung of the Dipnoi. Of every stage of the process here outlined, examples exist, and there is great reason to believe that the development of the lung followed the path above pointed out.

When the carboniferous era opened there may have been many lung- and gill-breathing Dipnoi, which spent much of their time on land, and some of which, by a gradual improvement in their organs of locomotion, changed into batrachians. But with the appearance of the latter, and of their successors, the reptiles, the relations of the fish to the land radically changed. The fin, or the simple locomotor organ of the Dipnoi, could not compete with the leg and foot as organs of land locomotion, and the fish tribe ceased to be lords of the land, where instead of feeble prey they now found powerful foes, and were driven back to their native habitat, the water. Nor did the change end here. In time the waters were invaded by the reptiles, numerous swimming forms appearing, which it is likely were abundant in the shallower shore line of the ocean, while they sent many representatives far out to sea. These were actively carnivorous, making the fish their prey, the great mass of whom were doubtless driven into the deeper waters, beyond the reach of their air-breathing foes.

In this change of conditions we seem to perceive an adequate cause for the loss of air-breathing habits in those fishes in which the lung development had not far progressed. It may, indeed, have been a leading influence in the development of

the Teleostean or bony fishes, as it doubtless was in the loss of its primitive function by, and the subsequent changes of, the air-bladder.

Such of the Ganoids and Dipnoi as survived in their old condition had to contend with adverse circumstances. Most of them in time vanished, while the Ganoids which still exist have lost in great measure their air-breathing powers, and the Dipnoi, in which the development of the lung had gone too far for reversal, have degenerated into eel-like, mud-haunting creatures, in which the organs of locomotion, which perhaps once served them efficiently for land travel, have become converted into the feeble paddle-like limb of Ceratodus and the filamentary appendages of the other species.

As regards the presence of a large quantity of oxygen in the bladders of deep-swimming marine fishes, it not unlikely has a respiratory purpose, the bladder being, as suggested by Semper, used as a reservoir for oxygen, to serve the fish when sleeping, or when, from any cause, not actively breathing. The excess of oxygen is not due to any like excess in the gaseous contents of sea-water, for the percentage of oxygen decreases from the surface downward, while that of nitrogen remains nearly unchanged. In all cases, indeed, the bladder may preserve a share of its old function, and act as an aid in respiration. Speaking of this, Cuvier says: "With regard to the presumed assistance which the swim-bladder affords in respiration, it is a fact that, when a fish is deprived of that organ, the production of carbonic acid by the branchiæ is very trifling," thus strongly indicating that the bladder still plays a part in the oxygenation of the blood.

Under the hypothesis here presented, the process of evolution involved may be thus summed up. Air-breathing in fishes was originally performed by the unchanged walls of the œsophagus, perhaps at specially vascular localities. Then the wall folded inward, and a pouch was finally formed, opening to the air. The pouch next became constricted off, with a duct of connection. Then the pouch became an air-bladder with respiratory function, and finally developed into a simple lung. These air-breathing fishes haunted the shores, their fins

becoming converted into limbs suitable for land locomotion, and in time developed into the lung- and gill-breathing batrachia, and these in their turn into the lung-breathing reptilia, the locomotor organs gradually increasing in efficiency. Of these pre-batrachia, we have existing representatives in the mud-haunting Dipnoi, with their feeble limbs. In the great majority of the Ganoid fishes the bladder served but a minor purpose as a breathing organ, the gills doing the bulk of the work. In the Teleostean descendants of the Ganoids the respiratory function of the bladder in great measure or wholly ceased, in the majority of cases the duct closing up or disappearing, leaving the pouch as a closed internal sac, far removed from its place of origin. In this condition it served as an aid in swimming, perhaps as a survival of one of its ancient uses. It gained also in certain cases some connection with the organ of hearing. But these were makeshift and unimportant functions, as we may gather from the fact that many fishes found no need for them, the bladder in these cases decreasing in size until too small to be of use in swimming; and in other cases completely disappearing, after having travelled far from its point of origin. In some other cases, above cited, the process seems to have begun again in modern times, in an eversion of the wall of the œsophagus for respiratory purposes. The whole process, if I have correctly conceived it, certainly forms a remarkable organic cycle of development and degeneration, which perhaps has no counterpart of similarly striking character in the whole range of organic life.